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Home ranges of lions in the Kalahari, Botswana exhibit vast sizes and high temporal variability

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ABSTRACT

The central Kalahari region in Botswana is one of the few remaining ecosystems with a stable lion population. Yet, relatively little is known about the ecology of the lions there. As an entry point, home range estimations provide information about the space utilization of the studied animals. The home ranges of eight lions in this region were determined to investigate their spatial overlaps and spatiotemporal variations. We found that, except for MCP, all home range estimators yielded comparable results regarding size and shape. The home ranges of all individuals were located predominantly inside the protected reserves. Their areas were among the largest known for lions with 1131 – 4314 km^2 (95 %), with no significant differences between males and females. Numerous overlaps between lions of different sexes were detected, although these originate from different groups. A distance chart confirmed that most of these lions directly encountered each other once or several times. Strong temporal variations of the home ranges were observed that did not match a seasonal pattern. The exceptionally large home ranges are likely to be caused by the sparse and dynamic prey populations. Since the ungulates in the study area move in an opportunistic way, too, strong spatiotemporal home range variations emerge. This can lead to misleading home ranges. We therefore recommend clarifying the stability of the home ranges by applying several levels of temporal aggregation. The lack of strict territoriality is likely an adaptation to the variable prey base and the high energetic costs associated with defending a large area.

KEYWORDS

Home range; lion; Kalahari; biased random bridges; time local convex hull

1 INTRODUCTION

Through differential patterns of predation, apex predators are important agents of ecological and evolutionary processes (Berger et al., 2001; Duffy, 2002; Ale and Whelan, 2008; Pitman et al., 2012). However, large predators such as lions are frequently in direct competition with humans and, where their distributions overlap, are perceived as a threat to the health and welfare of people (Patterson et al., 2004; Bauer and de Iongh, 2005; Schiess-Meier et al., 2007). Consequently, large mammalian predators are in global decline (Inskip and Zimmermann, 2009; Bauer et al., 2012; Ripple et al., 2014).

The central Kalahari region of Botswana is one of the few remaining areas where lion populations are relatively stable and represents a globally important conservation area for the species (Bauer and Van Der Merwe, 2004; Winterbach et al., 2014). However, this dry savannah area offers a poorly understood, dynamic habitat where important resources are scarce and widely dispersed (Dawson and Butynski, 1975; Funston, 2011). Home range analysis serves as a key entry point to define the interaction between animals and their habitat (Marker and Dickman, 2005; Downs and Horner, 2008; Tumenta et al., 2013). It helps to explore the nature and extent of the human-predator conflict and therefore to inform conservation programmes (Mizutani and Jewell, 1998; Bauer and de Iongh, 2005; Graham, Beckerman and Thirgood, 2005; Kolowski and Holekamp, 2006; Lehmann et al., 2008; Loveridge et al., 2009; Schuette et al., 2013; Tumenta et al., 2013). Hence, numerous studies are available concerning the computation of home ranges. Typically, one or two appropriate home range estimators are selected and used to determine the location and area of a species' home range (Spong, 2002; Bauer and de Iongh, 2005; Marker and Dickman, 2005; Loveridge et al., 2009; Bothma and Bothma, 2012).

However, it is difficult to decide which method is most suitable for a given study. Since the performance of a home range estimator has typically been evaluated on the basis of simulated data and thus strongly depends on the utilised simulation, the findings of different studies are

often contradictory (Getz and Wilmers, 2004; Getz et al., 2007; Lichti and Swihart, 2011; Wall et al., 2014). In addition, simulated home ranges rarely reflect those of free-ranging animals (Horne and Garton, 2006; Downs and Horner, 2008). Another issue frequently found in home range studies is the implicit assumption that home ranges are stable over time, by computing them based on a single time period. Exceptions exist (Marker and Dickman, 2005; Loveridge et al., 2009; Tumenta et al., 2013), but are typically restricted to the presence of seasonal patterns of the home range size.

This study investigates the home ranges of eight lions in the Kalahari region of Botswana. Several home range estimators, including Minimum Convex Polygon (MCP), Kernel Density Estimation (KDE), Time Local Convex Hull (T-LoCoH) and Biased Random Bridges (BRB), were used to assess the influence of the home range estimator and to give a robust idea of the results. The home ranges were first analysed in terms of size and shape based on a single time period. In order to look for seasonal patterns and to investigate the stability of the computed home ranges, a second set of home ranges were computed using temporal subsets that match the climatic seasons.

2 MATERIALS AND METHODS

2.1 Study area

The study area is situated in the central Kalahari region in Botswana, between 22.5 – 24.5° S and 23.0 – 26.0° E (Fig. 1). It encompasses both the Khutse Game Reserve (KGR) and the Central Kalahari Game Reserve (CKGR) just north of KGR (Weilenmann et al., 2010). The game reserves are separated from the adjacent grazing areas by a fence along their south-eastern border (Schiess-Meier et al., 2007; Mills and Schiess-Meier, 2009; Mishra et al., 2015). However, the ease with which lions and other animals dig holes in the sandy substrate means that this barrier is relatively permeable (Kesch et al., 2014). The study area has a semi-arid climate, with a cold and dry season during the austral winter (June – September) and a warm and wet season during summer (November – April) (Department of Meteorological Services; Weilenmann et al., 2010; Leopard Ecology & Conservation, 2014). The mean monthly precipitation lies between 0 and 10 mm during winter and increases to 60 – 80 mm during summer months. The mean monthly temperature also shows seasonality and varies between 12 °C and 25 °C. The diurnal variation is quite pronounced and often higher than the seasonal differences (Department of Meteorological Services, 2016). The flat terrain of the study area is covered by a mixture of open herbaceous and open scrubland vegetation (Food and Agriculture Organization of the United Nations, 2016; Weilenmann et al., 2010; Mishra et al., 2015).

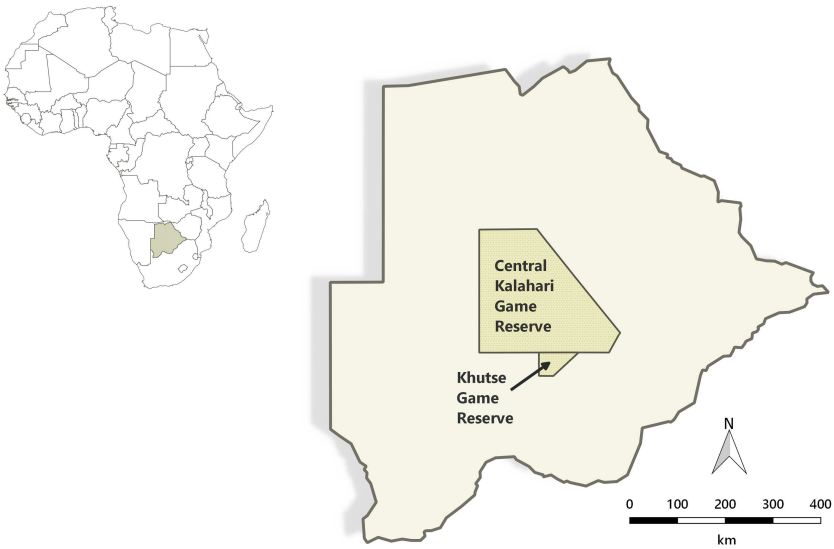

Figure 1 Location of the study area. The map shows the location of Botswana within the African continent and the two game reserves in the study area.

2.2 Data source

The telemetry datasets of the lions were collected over a 4.5-year period as part of an ongoing study of large felid predators conducted by Leopard Ecology & Conservation (Gaborone, Botswana). From these, incomplete records without coordinates, timestamps or dilution of precision (DOP) values were removed. If one of these attributes contained an invalid or, in the case of DOP, a too high value, the corresponding record was deleted as well. We followed the proposition of Lewis et al. (Lewis et al., 2007) and used a cut-off value of 10.0 for the DOP. In order to be included in the subsequent analyses, the datasets filtered this way had to meet three criteria: at least one year of records, no gaps (i.e. no period of missing fixes) longer than one week occur, and all of the datasets intersect temporally. Table 1 shows the datasets of the eight individuals that fulfilled all criteria. Detailed information on the lions included in this study and their social structure can be found in the supplementary material. The GPS positions were recorded by using GPS Plus Iridium collars (VECTRONIC Aerospace, Berlin, Germany) for all lions. The sampling interval over the tracking period is irregular for some individuals and varies between 25 and 270 minutes (due to missing fixes). Most often, however, sampling intervals between 30 and 60 min occurred.

Table 1 Characteristics of the investigated lions. The tracking periods of most individuals overlap temporally by one year or more.

Individual	Sex	Sampling intervals [min]	Tracking period
LF12	F	30	20 Aug 2011 – 02 Sep 2013
LF13	F	30, 60	21 Aug 2011 – 06 Aug 2014
LF16	F	30, 60	10 Jul 2012 – 08 Sep 2014
LF14	F	30, 60	22 Dec 2011 – 04 Sep 2014
LF07	F	30	22 Apr 2011 – 09 Feb 2013
LM06	M	30, 60	09 May 2012 – 26 Mar 2014
LM07	M	30	21 Sep 2012 – 06 Sep 2014
LM08	M	30, 60	29 Nov 2012 – 08 Sep 2014

2.3 Home range estimation

2.3.1 Choice of home range estimators

Four methods were applied to estimate the home ranges: minimum convex polygon (MCP), location-based kernel density estimation (KDE), time local convex hull (T-LoCoH) (Lyons et al., 2013) and biased random bridges (BRB) (Benhamou, 2011). Each method was applied to each dataset to compute the respective utilization distribution (UD), 95 % home range isopleth (subsequently designated as 'home range') and the 50 % home range isopleth (designated as 'core area'). MCP and KDE were selected because they are the most frequently used home range estimators (HRE) and therefore important baselines for comparisons (Millspaugh and Marzluff, 2001; Downs and Horner, 2008; Lichti and Swihart, 2011). T-LoCoH and BRB are more sophisticated methods that incorporate the temporal dimension but are still manageable for routine ecological analyses with regard to complexity of parameterization. Since the performance of a HRE depends highly on the spatial distribution of the data points and therefore on the concrete dataset used (Getz and Wilmers, 2004; Horne and Garton, 2006; Downs and Horner, 2008; Lichti and Swihart, 2011), it is expected that the usage of four different methods provides a sound idea of the possible range of results for this kind of data. Detailed information on the functioning of the HRE can be found in Millspaugh and Marzluff (2001), Burgman and Fox (2003), Börger et al. (2006) for MCP, Seaman and Powell (1996), Millspaugh and Marzluff (2001), Keating and Cherry (2009) for KDE, Getz and Wilmers (2004), Getz et al. (2007), Lyons et al. (2013), Dürr and Ward (2014) for T-LoCoH and Horne et al. (2007), Codling et al. (2008), Benhamou (2011), Dürr and Ward (2014) for BRB.

2.3.2 Preliminary analyses: parameterization

Preliminary analyses were conducted to test the influence of the parameterization of the respective HRE. MCP has no parameters other than the percentage of points farthest from the centroid that should be excluded. For the home range, this value was set to 5 %, whereas it was set to 50% for the core area. For KDE, it was found that the reference bandwidth method (REF) yielded the same results as biased cross-validation (BCV) and lead to slightly oversmoothed home ranges. The smoothed cross-validation (SCV) and solve-the-equation plug-in (PI) approaches were tested as well. Both of them performed almost identically and consistently led to highly fragmented home ranges (Fig. S1 in the supplementary online Appendix). Least square cross-validation (LSCV) failed to compute a result for several datasets due to high point densities and was thus excluded from the analysis. Other studies came up with similar observations in this regard (Hemson et al., 2005; Gitzen et al., 2006). Consequently, REF was used as a bandwidth estimator for KDE in combination with a Gaussian fixed kernel. Information on the bandwidth estimators can be found in Jones et al. (1996), Duong and Hazelton (2005), Hemson et al. (2005), Gitzen et al. (2006).

For T-LoCoH, the neighbourhood rule and the time parameter s had to be set. Preliminary analyses showed that the k-method suited our datasets better than the a-method, as the latter produced home ranges and core areas that have a low degree of spatial detail (Fig. S2). Lyons et al. (2013) recommended a value around 60 % for the time parameter s. Thus, the home ranges were initially computed using 40 %, 60 % and 80 % for this parameter. It was found that the difference between these values was of a minor importance (Fig. S2), so that the combination of an s-value of 60 % and the k-method was selected for the analyses. Since there is no optimal value for k, a wide range of potential results exist that may differ markedly. Thus, two T-LoCoH results were computed per individual: One that uses a k-value close to the lower end of the meaningful spectrum and a second one that lies close to the upper end. The mean of the two results was then designated as the final result of T-LoCoH.

The BRB approach is based on the equation from Benhamou and Cornélis (2010) and Jay et al. (2012) to determine the smoothing parameter (h_{min}). In this equation, half the distance that can be covered by an animal over an extended period of time using its maximum transit velocity is added to the uncertainty of the GPS collar (Benhamou and Cornélis, 2010; Jay et al., 2012). To obtain this distance, the parts of each dataset being sampled regularly with the main sampling interval (30 min or 60 min) were analysed. The velocities between the GPS fixes were then calculated and sorted, and the value of the 99th percentile was multiplied with the sampling interval. Then, half this distance was added to the 30 m of the uncertainty component to obtain the value for h_{min}. Preliminary analyses revealed that the resulting home range estimates were too fragmented (Fig. S3). Thus, to remedy this, scaling factors between 1.4 and 2.2 had to be applied (Table S1).

2.4 Home range evaluation

The home ranges and core areas were evaluated in terms of their area and shape. For the latter, the compactness measure S of Ebdon (1985) was used, which is the ratio of the areas of the home range isopleth and the smallest circumcircle that contains the whole isopleth. A value of 1 for S means that the object's shape equals a circle. It is an indicator of the ecological efficiency, since a circle has the lowest perimeter for a given area (Ebdon, 1985).

To determine the degree of spatial intersection between coexisting individuals, the volume of intersection (VI) was used, an index that applies the idea of an intersection of the utilization distributions and ranges between 0 (no overlap) and 1 (complete overlap) (Millspaugh et al., 2004; Fieberg and Kochanny, 2005). Other than the conventional overlap between home range isopleth polygons, the VI index takes into account how frequently the overlapping regions have been used by the animals (Fieberg and Kochanny, 2005; Gitzen et al., 2006). Since a UD is required, the VI index was computed only for KDE and BRB. The final VI value is the average of these two results.

The analysis of the size and shape was conducted for the home ranges and core areas derived from the whole dataset and also from the respective seasonal subsets for each study animal. The seasons were defined relative to the local climate and were split into a summer (November – April) and a winter season (June – September). For each season of each year, a single home range and core area was determined using KDE in combination with the reference bandwidth. Since this combination tends to oversmooth more than the other estimators, it has the lowest likelihood of erroneously indicating changes over time that are solely artefacts of the home range estimators.

2.5 Implementation

All analyses were carried out in R (R Core Team, 2015). The package *adehabitatHR* was used for MCP and KDE, *adehabitatLT* for BRB. T-LoCoH was computed by using *T-LoCoH*. *Tripack* provided the functions for the compactness shape measure. The coordinates of all datasets were converted from WGS84 (EPSG: 4326) to the projected spatial reference system Cape / UTM zone 36S (EPSG: 22236) prior to all analyses.

3 RESULTS

3.1 Overall home range estimation

3.1.1 Trends of the home range estimators

KDE, T-LoCoH and BRB yielded core area and home range estimates that are often very similar regarding their size and shape, particularly when being compared to the results of MCP (Tables S2 and S3). On average, differences of 10 % ± 5 % for the area and 16 % ± 13 % for the shape of the home ranges exist between the smallest and the largest value of

KDE, T-LoCoH and BRB. For the core area, average differences of 17 % ± 10 % were detected for the area. The compactness indices, however, varied more strongly, with average differences between the lowest and highest value of 41 % ± 24 %. Neither the area nor the compactness showed a consistent pattern in values derived from KDE, T-LoCoH and BRB.

MCP consistently produced the most compact home ranges and core areas, as this method is designed to generate convex polygons. The average compactness index of KDE, T-LoCoH and BRB is only 39 % ± 9 % of that computed by MCP (Tables S2 and S3). The discrepancy is smaller for the home range but still considerable (61 % ± 7 %). MCP also yielded the largest areas for both isopleths in most cases. The mean area of KDE, T-LoCoH and BRB is 80 % ± 10 % for the MCP core area and 87 % ± 7 % for the home range. However, MCP did not yield the largest area in two cases for the core area and in one case for the home range.

3.1.2 Individual home ranges and core areas

The locations of the home ranges (95 % isopleth) are shown in Figs. 2 and 3. For comparison Figs. S4 and S5 depict the corresponding core areas (50 % isopleth). With a maximum percentage of 3.8 % for LF14, none of the eight home ranges exceed the boundary of the game reserves noticeably. The average home range size of the five results per individual varies between 1131 and 4317 km^2 (mean: 2682.5 ± 1037.6 km^2), and that of the core area (50 % isopleth) varies between 187 and 1061 km^2 (mean: 563.9 ± 281.6 km^2) (Table 2). The mean compactness of the home ranges is 0.52 ± 0.07, that of the core areas is 0.38 ± 0.09. Due to the convexity assumption of MCP, its home range estimates were not included in the computation of the average compactness measures. The compactness values are significantly higher for the home range than for the core area (U: 8, df: 14, p: 0.0134). They are also higher for the males than for the females but not statistically significant (home range: U: 2.5, df: 6, p: 0.1745, core area: U: 4, df: 6, p: 0.3682). The core areas are 20 – 31 % of the size of the 95 % boundaries for most lions. The female LF14 and the male LM07, however, are exceptions to this, with much lower ratios (14 % and 11 %). The detailed results per HRE can be found in Tables S2 and S3. Both the smallest and largest areas were obtained by male individuals, whereas those of the females lie between these extremes (home range: 2090 – 3431 km^2, core area: 427 – 789 km^2). An influence of the sample size or the time span over which fixes have been recorded does not seem to play a major role since the individuals with the largest and smallest values all have almost identical datasets in these regards. No significant difference of the area due to the sex could be determined (Mann-Whitney U) for the core area (U: 10, df: 6, p: 0.570) or the home range (U: 10, df: 6, p: 0.570).

Table 2 Mean area and compactness values. The averages of the five home range estimates per individual (± SD) are presented. The highest value is printed in bold and the lowest is indicated in italics. Note that the MCP result was ignored for the average compactness.

	Core area (50 %)		**Home range (95 %)**	
Individual	**Area [km2]**	**Compactness**	**Area [km2]**	**Compactness**
LF12	746.6 ± 73.3	0.37 ± 0.20	3277.8 ± 219.8	0.50 ± 0.01
LF13	473.4 ± 57.6	0.37 ± 0.12	2411.8 ± 125.9	0.57 ± 0.03
LF16	788.7 ± 122.0	0.33 ± 0.03	3093.8 ± 193.0	0.52 ± 0.02
LF14	482.3 ± 153.1	0.26 ± 0.17	3430.6 ± 619.0	0.50 ± 0.03
LF07	427.1 ± 29.8	0.40 ± 0.06	2090.2 ± 95.2	0.39 ± 0.10
LM07	187.2 ± 19.1	**0.56 ± 0.07**	1707.0 ± 132.1	0.53 ± 0.07
LM06	**1061.4 ± 83.7**	0.31 ± 0.06	**4317.4 ± 361.6**	0.52 ± 0.01
LM08	344.1 ± 26.6	0.45 ± 0.02	1131.1 ± 50.2	**0.63 ± 0.02**

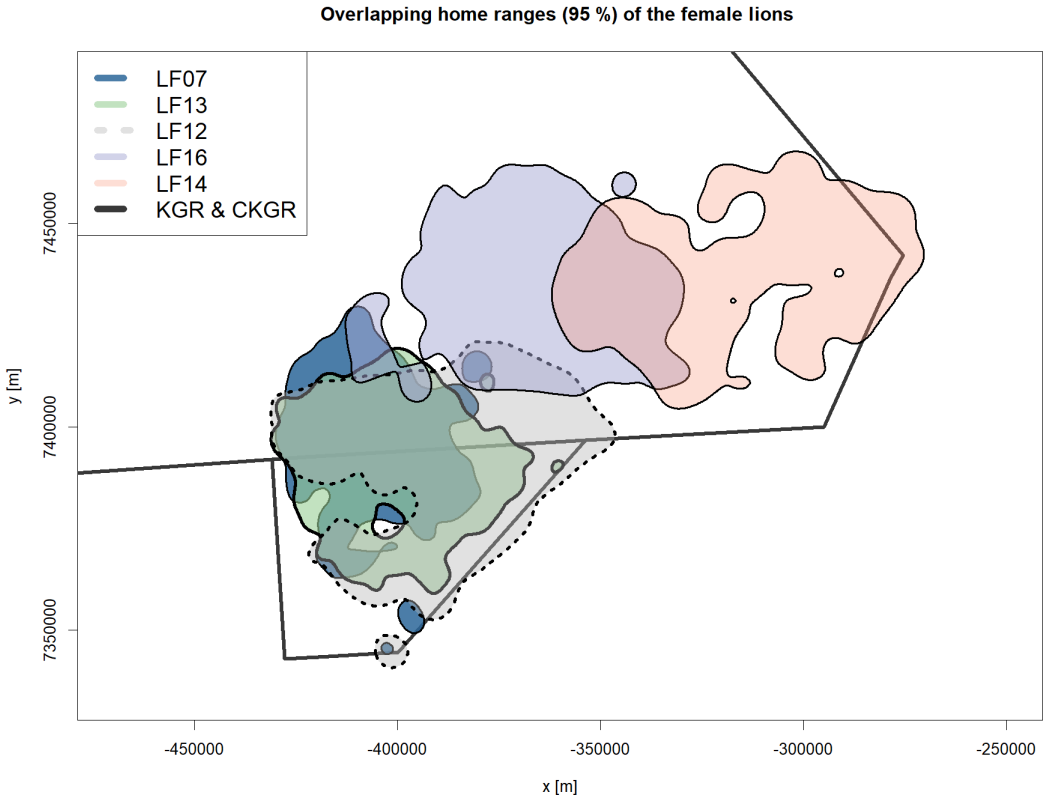

Figure 2 Visualized home ranges (95 % isopleth) of the female lions. The combination of KDE and the reference bandwidth is presented.

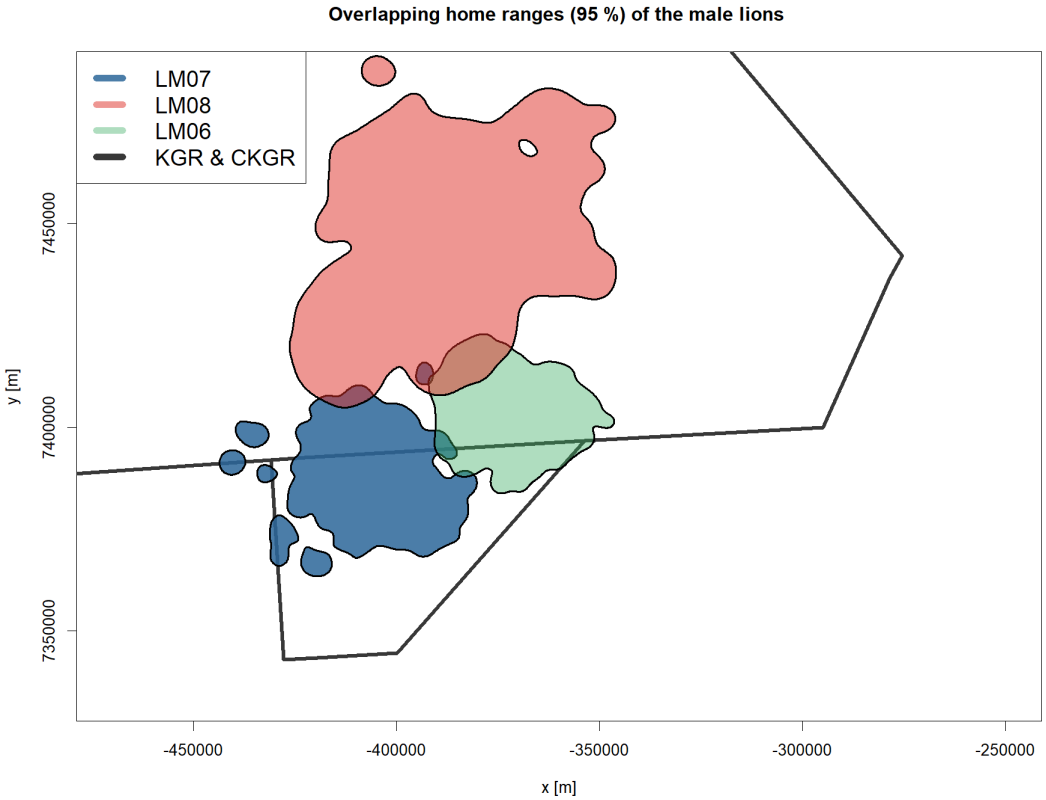

Figure 3 Visualized home ranges (95 % isopleth) of the male lions. The combination of KDE and the reference bandwidth is presented.

3.1.3 Conspecific interactions

Table 3 presents the values for the volume of intersection, which indicates the degree of spatial overlap. The home ranges of the males hardly intersect each other, with VI values below 5 %. Intersecting home ranges were much more frequent for the lionesses, however. Particularly LF13 and LF07 (62 %), as well as LF12 and LF13 (41 %) have UDs with a high degree of overlap. High VI values also occurred between males and females, such as between LM08 and LF12 (54 %), LM07 and LF07 (47 %) or LM07 and LF13 (42 %). The Euclidean distances shown in Table 4 further differentiate these overlaps. These distances were computed for all pairs of individuals, with a VI value of 20 % or higher by looking at GPS fixes that have a time lag of 60 minutes or less. The minimum values as well as the 10 %, 25 % and 50 % quantiles are presented. The values of Table 4 reveal that nearly all of the analysed pairs of individuals have minimum distances close to 0 km. Only LM07 and LF12 have a substantially larger minimum distance of 5.5 km. LF12 and LF13, LM08 and LF12 as well as LM07 and LF13 have small distances up to their 10 % and partially even 25 % quantiles.

Table 3 Mean volume of intersection [%] of the utilization distributions. The average of the index values of KDE and BRB per individual is shown. Females are underlined.

	LF12	**LF13**	**LF16**	**LF14**	**LF07**	**LM06**	**LM07**	**LM08**
LF12	100	41	6	0	28	4	21	54
LF13	41	100	2	0	62	3	42	11
LF16	6	2	100	26	4	29	1	12
LF14	0	0	26	100	0	2	0	0
LF07	28	62	4	0	100	9	47	5
LM06	4	3	29	2	9	100	1	4
LM07	21	42	1	0	47	1	100	3
LM08	54	11	12	0	5	4	3	100

Table 4 Spatiotemporal, concurrent distances between the lions. The minimum value and different quantiles of the Euclidean distances between pairs of lions at similar timestamps are shown. A maximum time lag of 60 minutes was allowed between GPS fixes of the two individuals in order to include them in the computation.

Pair of lions	**Minimum [km]**	**10 % quantile [km]**	**25 % quantile [km]**	**50 % quantile [km]**
LF12 – LF13	0.0	0.0	0.0	23.2
LF12 – LF07	0.0	7.9	17.8	28.1
LF13 – LF07	0.0	6.4	12.0	20.1
LF16 – LF14	0.2	16.4	23.7	36.8
LM07 – LF12	5.5	19.4	25.6	35.6
LM07 – LF13	0.0	0.5	11.8	18.2
LM07 – LF07	0.7	12.4	18.9	26.2
LM06 – LF16	0.0	12.6	23.5	36.0
LM08 – LF12	0.0	0.0	0.3	6.9

3.2 Seasonal home range estimation

The home ranges computed at a seasonal scale show a high degree of temporal variability of the areas for most individuals (Fig. 4; see Fig. S7 for the corresponding maps). The home range area of LF14 increased constantly over four seasons from 268 km^2 to 3626 km^2 and thus expanded by a factor of 13.5 (Fig. 5). LF12, on the other hand, showed a constant decrease over time from 3063 km^2 to 788 km^2, linked to a shift in north-eastern direction. A decreasing area was also detected for LF13, but without a noticeable shift in a particular direction. For LM06, whose home range area decreased sharply in winter 2013, the static area of 4317 km^2 is larger than any of the seasonal values (1316 – 3802 km^2). Not only the area but also the shape of the home ranges changed over time. With magnitudes below 2, however, the changes are less pronounced (Fig. S6). For three of the lions (LF12, LF16 and LM08) the compactness increased during each summer, while only one individual (LM07) showed the opposite trend. The core areas show similar trends in terms of area and shape over time as the 95 % isopleths do, and are thus not shown.

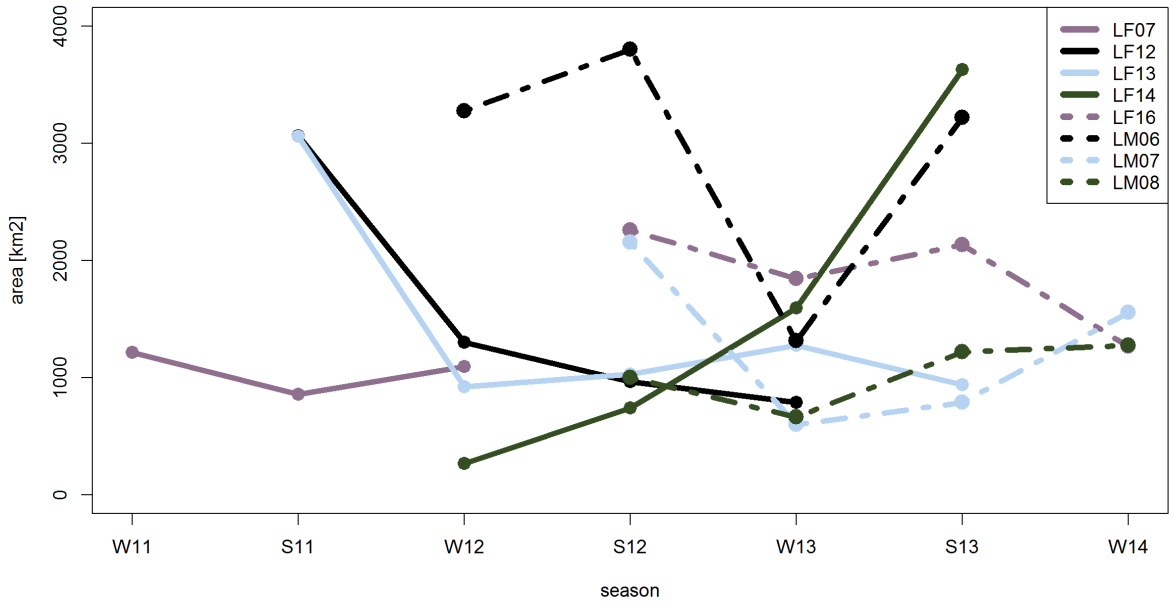

Figure 4 Temporal variability of the home range area (95 %). *W* denotes the austral winter season (June–September), *S* the austral summer season (November–April). The subsequent number designates the year (2011–2014).

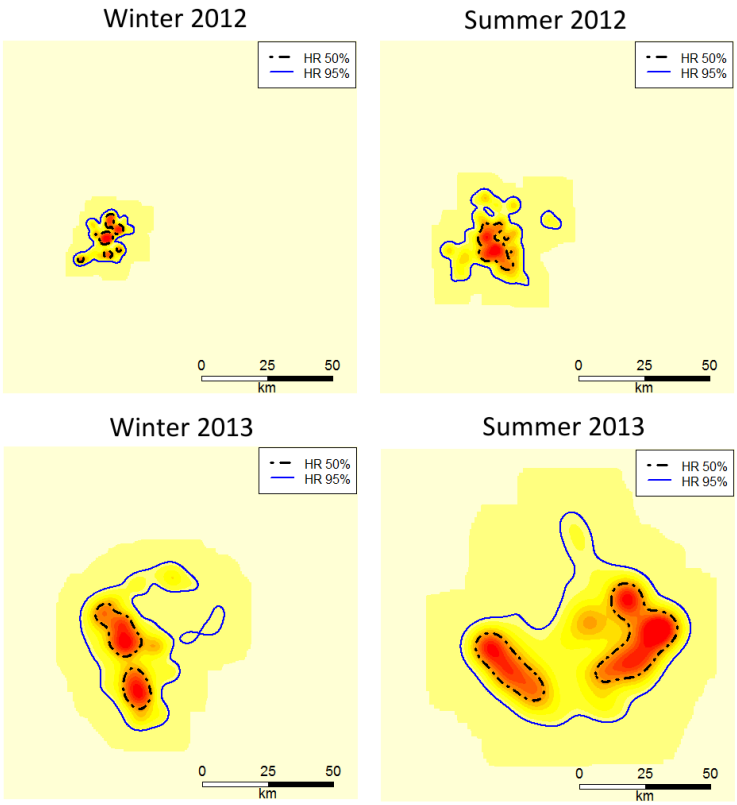

Figure 5 Spatiotemporal variation of LF14's home range. After winter 2012 a nearly exponential increase in size primarily directed to the northeast could be observed. The same spatial reference frame was used for all of the individual images.

4 DISCUSSION

4.1 Trends of the home range estimators

The fact that MCP produced the largest home range estimates is in agreement with the literature (Börger et al., 2006; Huck et al., 2008; Hull et al., 2015). Since MCP implicitly assumes a home range to be convex, it depends strongly on the spatial distribution of the samples (Seaman et al., 1999; Downs and Horner, 2008). This is illustrated by the overall home range of LF14 (Fig. 2), which does not meet the convexity assumption and presents a large discrepancy between the area estimates of MCP and the other methods. However, despite producing the largest area estimates, MCP should not be used to obtain conservative estimates for purposes such as the protection of species, as suggested by Huck et al. (Huck et al., 2008). This is illustrated by the resulting core area of MCP, which overlaps the core areas of the other HREs only to 54 % on average, with extreme values as low as 29 % for one individual (LF14). This means that although a sufficiently large area would be protected, it may not be the most important area for the animal. For the 95 % isopleth, the situation is less critical, with overlaps of 79 % on average (LF14: 64 %), but still far away from congruency.

Except for the compactness of the core area, the results obtained by using KDE, T-LoCoH and BRB are similar regarding their size and compactness. Particularly the often-used 95 % area size can be designated as reasonably stable on average. Nevertheless, as shown for the data of LF14 or LM07, significant differences between these three HREs can arise as well. Using more than one method can therefore allow a more comprehensive view on the home ranges and core areas and their range of possible forms.

4.2 Home range sizes

Both the home ranges (mean 2682.5 ± 1037.6 km^2, max 4317 km^2) and the core areas (mean 563.9 ± 281.6 km^2, max 1061 km^2) are exceptionally large. The only published reports of home ranges with comparable sizes stem from the Kgalagadi Transfrontier Park (1500 – 4500 km^2), a protected area that is also part of the southern African Kalahari region (Hayward et al., 2009; Funston, 2011; Tumenta et al., 2013). In more humid areas, the home ranges are much smaller. For instance, in the Waza National Park in Cameroon (537 – 1534 km^2), the Kunene region in the northwest of Namibia (up to 1628 km^2) or the Makgadigadi Pans National Park northeast of the CKGR in Botswana (up to 1143 km^2) (Bauer and de Iongh, 2005; Hayward et al., 2009; Tumenta et al., 2013).

4.3 Conspecific interactions

Males are often reported to have larger home ranges than females, even though these differences are only rarely statistically significant because of the low number of individuals studied and the high variability between them (Hayward et al., 2009; Loveridge et al., 2009; Tumenta et al., 2013). Such a sex-specific disparity could not be found in this study.

According to the obtained volume of intersection values, some of the lionesses shared their home range with other males and females, although data from regular resightings suggest that all of the females belong to separate groups. The home ranges of the three males did not intersect each other, which indicates that they belong to different prides (Spong, 2002; Haas et al., 2005). Due to the long time period on which the VI values are based, and the fact that this concept ignores the temporal dimension, pairs of lions may have a high degree of spatial overlap but nonetheless never have met directly. According to the minimum values of the Euclidean distances (Table 4), however, most pairs of individuals likely encountered at least once. Considering the temporal uncertainty (maximum time lag of 60 minutes), the minimum distances of 0.7 km for LM07 and LF07 as well as 0.2 km for LF14 and LF16 may be artefacts. Only for LM07 and LF12 it is, despite their VI value of 21 %, unlikely that they met directly, since their smallest recorded distance is 5.5 km. The opposite is the case for LF12 and LF13, LM08 and LF12, as well as LM07 and LF12, which have small distance values even for their 10 % and partially also 25 % quantiles. Thus, these individuals spent a certain amount of time in close proximity to one another.

4.4 Spatiotemporal variability

Temporal variations in size and shape of home ranges were pronounced for most individuals and resulted in seasonal home range estimates that differ markedly from the static estimate. Particularly the size of both the home range and core area varied considerably over time. However, consistent seasonal patterns in these home range metrics could not be detected. Regarding the size of the home ranges, this is in agreement with the findings of Ramsauer (2006), who investigated the home ranges of lions in the same study area during the years 2003 to 2006. The shapes of the home ranges are variable as well, but to a lesser degree. However, the shape was determined by using only a single compactness measure. Alternative and more complex measures may more accurately identify the changes in the shape of the home ranges, e. g. for LF14.

Given the strong spatiotemporal variation of our lion home ranges, a single static measure can hardly represent the area required by an animal appropriately. As demonstrated by the home range of LF14 (Fig. 5), home range sizes may therefore be overestimated. Or, depending on the observed time span, also underestimated. A lack of such variation may be one of the reasons for the markedly smaller home range estimates of Ramsauer (2006), who obtained values of only 604 – 861 km^2 (mean: 838 ± 421 km^2) in the same study area under comparable environmental conditions. The large discrepancy of the obtained home range

sizes, however, clearly shows the need to consider the temporal dimension for home range analyses, so that such issues can be resolved. This will allow for deeper insights into the ecology of the studied animals and also support meaningful comparisons of results from different studies.

4.5 Ecological implications

The extreme size of the home ranges recorded in this study and the lack of size differentiation between the sexes suggests that one or more critical resources are highly dispersed. Given the homogenous topography and wooded nature of the savannah landscape, vegetation cover is ubiquitous. Consequently, the principle life requisite resources most likely to be limiting are water and food (prey) (Macdonald, 1983; Spong, 2002; Lehmann et al., 2008). Perennial surface water is only available at specific, artificially supplied waterholes. Hence water is predictably localised in the study area. Therefore, it is assumed that it is the availability of prey that determines the extent of the observed home ranges (Eloff, 1998). Lion prey distribution within the dry Kalahari savannah system is characterised by the opportunistic movements of most ungulates (Bergström and Skarpe, 1999) in response to heterogeneous, episodic rainfall and infertile soils (Aranibar et al., 2004). This assumption is supported by the distribution of kill sites of these lions, which are widely dispersed across the extent of home ranges and are only moderately concentrated within the core area (Zehnder, 2015). The acquisition of sufficient prey for a lion group requires large, temporally variable home ranges.

Lions are regarded as territorial species, the extent of the territory is thus closely linked to the UD of the pride (Schaller, 1972; Funston et al., 2003; Packer et al., 2005) and its integrity is maintained by both resident males and females (McComb et al., 1994; Grinnell and McComb, 1996; Mosser and Packer, 2009). Territoriality serves two primary purposes linked to reproductive fitness: it confers a degree of exclusivity in accessing habitat resources, particularly limiting or key resources. It also provides access to individuals of the alternative sex with a diminished risk of infanticide that is frequently the consequence of a change in male tenure of a pride (Schaller, 1972; Macdonald, 1983; Maher and Lott, 2000; Mosser and Packer, 2009). Hence, the size, shape and location of the home ranges are, in addition to the distribution of critical resources, also influenced by the social landscape. The concept of territoriality is supported by the minimal overlap of male-male UDs. However, the UDs of female lions overlap substantially with that of males and females belonging to different social groups. These results challenge the assumption that lion territories occupy the extent of the home range and that both male and female lions consequently defend their pride's territory (Eloff, 1998; Spong, 2002).

Considering the large extents of the lion home ranges and core areas recorded here, the energetic cost associated with the maintenance of the entire area as an exclusive territory will be immense. This is exacerbated by prey resources that occur at low densities or are widely dispersed. It is therefore unlikely that the home ranges in this study can be entirely defended. If large home ranges are an environmental necessity and defended range areas a social requirement, a circular territory would offer the greatest resource area with the least edge within a homogeneously accessible landscape such as it is the case here. The fact that most compactness values are significantly larger for the 95 % than the 50 % isopleth, particularly amongst the males, indicates that there is a tendency toward efficient home range boundaries. However, the range in compactness values implies that the extensive home range is not optimised for territorial defence.

5 CONCLUSIONS

While MCP home ranges were significantly larger than other home range estimates with a low spatial correspondence, the KDE, T-LoCoH and BRB methods yielded comparable

results. However, the performance of these methods may vary depending on the input data, hence the use of different estimators is advisable to derive a robust interpretation of range use patterns.

The observed lions have home ranges that are among the largest recorded for the species. This is assumed to be a consequence of the environmental conditions of the Kalahari. Similarly, the pronounced spatiotemporal variability of the size and shape of home ranges is interpreted as a consequence of the dispersed and dynamic large herbivore community. Depending on the time span considered for a home range analysis, the obtained home ranges may differ significantly, as the comparison with Ramsauer (2006) indicates. It is thus essential to investigate home ranges over extended periods of time and at different temporal aggregation levels to determine the extent of the spatiotemporal variability.

Extensive home range areas and a high degree of spatiotemporal variability in these, represent challenging conditions for a territorial species. Our data suggest that under these circumstances, Kalahari lion prides may not defend the greater part of their static home range. They may maintain exclusive use of a smaller part of the home range, which captures critical resources, such as perennial surface water, and optimises the relation between the greatest area to encompass sufficient prey and the least defended edge. Alternatively, the defended area may vary temporally, in response to shifting resources and range use patterns. These are aspects of Kalahari lion biology that require further study.

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APPENDIX A. SUPPLEMENTARY DATA

Supplementary data associated with this article can be found, in the online version, at doi: ###.

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